GUIDELINES FOR PROTECTING MARBLED SALAMANDERS AND THEIR HABITATS IN MASSACHUSETTS

Natural Heritage and Endangered Species Program
Massachusetts Division of Fisheries and Wildlife
Route 135, Westborough, MA 01581
Author: Suzanne Fowle
Last updated: 8 February 2001

INTRODUCTION

The Natural Heritage and Endangered Species Program of the Massachusetts Division of Fisheries and Wildlife (the Division) has developed the following guidelines to assist property owners, land managers, consultants, and conservation commissioners with protecting marbled salamanders (*Ambystoma opacum*) and their habitats. The marbled salamander is listed as Threatened by the Division in Massachusetts, and activities proposed in or near its habitats are subject to review under Massachusetts laws. The Division intends to apply these guidelines in its review of Notices of Intent, pursuant to the Massachusetts Wetlands Protection Act regulations (310 CMR 10.59). Implementing these guidelines will also help property owners and land managers avoid potential violations of the Massachusetts Endangered Species Act (MGL c. 131A) and its implementing regulations (321 CMR 10.00).

Users of these guidelines are advised that they do not supersede any law, regulation, or official policy of this or any other agency. Rather, these guidelines are intended to complement existing regulatory review processes by providing scientifically based management recommendations. These guidelines include a summary of life history and habitat requirements of marbled salamanders, a summary of pertinent laws and regulations, guidelines for avoiding adverse impacts to marbled salamanders and their habitats, and literature cited.

LIFE HISTORY AND HABITAT REQUIREMENTS OF THE MARBLED SALAMANDER

Adult marbled salamanders spend most of their lives in dry, forested uplands, traveling to wetlands only during the breeding season, in the late summer and early fall (Table 1). Females lay their eggs, usually under leaf litter, in the depressions of dried seasonal pools, at the edges of reduced pools, and in small depressions under logs and vegetation that will be flooded by fall rains. Eggs hatch shortly after fall rains inundate the pool, and the aquatic larvae develop over the course of the fall, winter, and spring. In the early summer of the following year, larvae metamorphose and emerge as terrestrial juveniles.

Seasonal pools, often called “vernal pools,” are shallow, temporary wetlands. They dry up as often as once a year and therefore do not contain any fish, which prey on amphibian eggs and larvae. Marbled salamanders are considered "obligate" breeders in seasonal pools, meaning they depend on these fish-free habitats for successful breeding (the ecological trade-off is

that the larvae have to metamorphose relatively quickly, before the pool dries). Marbled salamanders may also breed in the dried-up edges of permanent wetlands, but few eggs or larvae are likely to survive if fish have access to that portion of the wetland.

Adult migration to breeding sites occurs in the late summer and early fall. Researchers in the Connecticut River Valley of Massachusetts found marbled salamanders migrating to breeding sites from mid-August through mid-October, with most males moving in late August and most females moving in early September (C. Jenkins, unpubl. data). Adult marbled salamanders may remain in or near their breeding sites for 2 to 67 days (Shoop and Doty 1972).

When gathered at breeding sites, marbled salamanders perform a courtship ritual. Males deposit spermatophores that fertilize females' eggs internally, once females pick them up. Additionally, Krenz and Scott (1994) found that a minimum of 31% of breeding females at one site were inseminated before reaching the egg-laying site, showing that some courtship occurs outside of wetland boundaries. Females construct a nest chamber – a small depression under leaf litter, a log, or a rock – in which they deposit eggs.

After breeding, males generally return to uplands before females, as many females initially remain with their clutches of eggs. In a study of several breeding pools in North Carolina, 52 to 100% of nests in each pool were attended by females, some into early November (Petranka 1990). Females leave their clutches as soon as fall rains inundate them, or by late November if the rains are not heavy enough to flood the pools. In a Massachusetts study, adults left the breeding site from early September through mid-November (C. Jenkins, unpubl. data).

Adults exhibit some fidelity to their migratory routes in and out of breeding sites and varying degrees of directionality (a common trend in the direction taken by all adults) (Shoop and Doty 1972, Douglas and Monroe 1981, Stenhouse 1985). Over 43% of adults in a population in Rhode Island exited their breeding site at the same place they entered (Shoop and Doty 1972). Entry and exit-routes occurred at various points along the edge of the pond, with most salamanders using a contiguous 225-degree section, or 63% of the pool's edge. However, in North Carolina, approximately 50% of adults exited within one 90-degree quadrant of the pool's edge (Stenhouse 1985). The same adults had entered the pool at random points.

Marbled salamanders can migrate long distances away from breeding pools (Table 2). Adult marbled salamanders in Indiana have been found to travel up to 450 m (average=194 m) away from a breeding site (Williams 1973). The author found that the maximum distance from breeding sites increased as the duration of the tracking study increased (from one year to two), and as the sample size increased (from 3 to 12).

Eggs usually hatch in the fall, if rains flood the nest. They then overwinter as aquatic, gill-bearing larvae, and continue their development in the spring. In a dry year, eggs may overwinter and then hatch in the spring (Bishop 1941, Morris 1991). Eggs reach hatching stage in a minimum of 15 days (Oliver 1955). Once they have developed to this stage, hatching depends on water levels at the nest site (Petranka et al. 1982). In Massachusetts,

marbled salamander eggs have hatched within three days of being inundated by rains (L. Gamble, pers. comm.).

Larvae develop into 60 to 75 mm-long, terrestrial juveniles in the late spring and early summer (Bishop 1943). Timing of metamorphosis varies geographically from March to July, but in Massachusetts the major pulse of emerging juveniles occurs in June (Bishop 1941, Williams 1973), at which point juveniles disperse both randomly and non-randomly. In South Carolina, juveniles dispersed from breeding ponds in random directions (D. Scott, unpubl. data). However, in North Carolina, 50% of emerging juveniles exited within one 90-degree quadrant of the pool's edge (Stenhouse 1985). Juveniles disperse as far as 1 km away from their ponds of origin (D. Scott, unpubl. data).

Table 1. General habitats required by the marbled salamander.

Habitat type	**Description**	**Time of year used by marbled salamanders (in Mass.)**
Breeding habitat	seasonal pools and other shallow wetlands	early August to mid-November (adults); mid-September to mid-July (eggs, larvae, and juveniles)
Non-breeding habitat	upland forest	year-round (adults and juveniles)

Table 2. Distances traveled by marbled salamanders away from breeding sites.

	Straight line distance (m)				
Life stage and location	**Minimum**	**Maximum**	**Average**	**No. of individuals (duration of study)**	**Source**
Adults					
Indiana	0	450	194	12 (2 seasons)	Williams 1973
Kentucky	not reported	not reported	30	6 (<1 season)	Douglas and Monroe 1981
Juveniles					
S. Carolina	10	1,000	not reported	(21 seasons)[1]	D. Scott, unpubl. data
Massachusetts[2]	30	945	not reported	55 (<1 season)	L. Gamble and C. Jenkins, unpubl. data

1 Data incidentally collected during a long-term drift-fence study of several wetlands. Total number of emergents trapped each year ranged from zero to 21,493, with an average of 2,753.
2 Distances moved were measured as straight-line distances between pitfall traps in which salamanders were caught. Although a total of 2,646 metamorphs were captured during this study, the information above is based on the 55 metamorphs that were recaptured at pools different from their pools of origin.

Age of sexual maturity is variable and ranges from 15 months (Bishop 1943) to >3 years after hatching (Scott 1994). Juvenile salamanders most likely remain in forested uplands during the breeding season, as do non-breeding adults.

The life history description above is based on a general seasonal framework within which marbled salamanders function, but it is not meant to be exact or predictable across all populations during all years. Even within the state of Massachusetts, marbled salamander activity varies from region to region each year. For example, breeding population sizes vary according to the numbers and sizes of emerging juveniles in previous years. The number of egg masses deposited in a breeding season varies according to the rainfall during that season, at that site. The number of embryos that survive to metamorphosis depends on rainfall, temperature (e.g. degree of freezing in pools), the abundance of predators, and other factors (Semlitsch et al. 1996).

***Threats to Marbled Salamanders* --** Marbled salamanders depend on more than the protection of habitats required by a single breeding population. Their persistence also depends on habitats that connect local populations to each other (Semlitsch and Bodie 1998). They appear to depend on a metapopulation dynamic to withstand fluctuating environmental conditions. A "metapopulation" is a population made up of several interacting "subpopulations," also referred to as "local populations." In the marbled salamander's case, the subpopulations are the breeding populations, each associated with a specific breeding pool or habitat. The metapopulation is the conglomerate of those breeding populations that are connected spatially (e.g. close enough together for salamanders to migrate and disperse between them).

If a local population declines or is extirpated -- due to drought, for example -- salamanders from neighboring subpopulations can eventually disperse into and repopulate the depleted subpopulation (see Semlitsch et al. 1996, Skelly et al. 1999). This is known as recolonization or the "rescue effect." The metapopulation dynamic is thereby, over time, a continuous "winking off" and "winking on" of breeding populations within a connected cluster of breeding populations. As a result, marbled salamanders may be absent from suitable breeding habitat one year, then recolonize that breeding site in subsequent years (Skelly et al. 1999).

When upland forest habitats connecting clusters of vernal pools are fragmented, local populations become isolated from each other, and the rescue effect becomes difficult or impossible to achieve (Laan and Verboom 1990, Reh and Seitz 1990). In addition, small, isolated populations are more vulnerable to a loss of genetic diversity and to random population fluctuations, both of which increase the likelihood of local extinction (Saccheri et al. 1998). Development activities that impede movements by salamanders are sources of habitat fragmentation, thereby degrading the viability of that population (potentially both the metapopulation and the local population) of marbled salamanders. Examples of potential impediments include roads, curbs, impermeable fencing, clear-cuts (deMaynadier and Hunter 1995), newly created waterways or permanent wetlands (adult marbled salamanders avoid standing water; Anderson 1967).

Other habitat alterations threaten marbled salamanders directly. In upland habitats, vehicles on roads and in parking lots will likely increase the mortality of adults and juveniles that overwinter, migrate, and disperse there. Roads across migration routes are especially

detrimental when salamanders are moving over them en masse to breed or as they emerge from pools (D. Scott, pers. comm.).

Marbled salamanders are found almost exclusively in forested areas where they burrow under leaf litter, logs, and topsoil (Williams 1973, Deegan and Berkholtz 1989). Therefore, clear-cutting, significant forest thinning, and removal and compaction of burrowing substrates degrades or destroys marbled salamander habitat (Raymond and Hardy 1991, deMaynadier and Hunter 1999). Ambystomatid salamanders readily use small mammal burrows (Williams 1973, Semlitsch 1981, Madison 1997), so the destruction or degradation of small mammal habitat likely adversely affect the quality of Ambystomatid habitat.

Adults feed on a variety of foods on the forest floor, including worms, snails, slugs, ants, beetles, and flies (Bishop 1941). Therefore, the removal of substrates used by invertebrates (such as downed woody debris) may adversely affect the quality of feeding habitat available to marbled salamanders.

Alteration of breeding sites can harm or kill adult and larval salamanders. Human disturbance at breeding sites in the fall -- such as walking on nest sites or disturbing the leaf litter covering a female and her clutch -- may cause females to abandon their nests (C. Jenkins, pers. com.), resulting in possible desiccation of the eggs (Petranka 1990). Altering the hydrology in marbled salamander habitats may also decrease the viability of marbled salamander populations. Shortening the hydroperiod at breeding sites can result in decreased body size of emerging juveniles. This in turn decreases the likelihood of survival to adulthood, delays sexual maturity, and decreases the viability of eggs if adulthood is reached (Scott 1990, Scott and Fore 1995, Taylor and Scott 1997). In the winter, spring, or early summer, when eggs and larvae are developing, the drawing-down of water can kill eggs and concentrate larvae into a pool too small to supply the nutritional requirements of the population (Scott 1990).

MASSACHUSETTS LAWS THAT PROTECT MARBLED SALAMANDERS AND THEIR HABITATS

Massachusetts Wetlands Protection Act – The Massachusetts Wetlands Protection Act (WPA) (MGL c. 131 s. 40) protects a variety of wetland "Resource Areas" (and, in some cases, the surrounding uplands) that can support rare, state-listed wildlife. According to the WPA's implementing regulations (310 CMR 10.00), projects that are proposed to occur in a Resource Area or associated 100-foot buffer zone, and that will alter wetland habitat of marbled salamanders or other rare wildlife, may have "no short or long term adverse effects" on that habitat. Specific protected Resource Areas that marbled salamanders are likely to inhabit include: Land Under Water Body; Isolated Land Subject to Flooding; Bordering Land Subject to Flooding; Bordering Vegetated Wetlands; and Riverfront Areas (Table 4). These are defined in detail in the WPA regulations.

The Division has prepared an atlas of "Estimated Habitats of Rare Wildlife," including estimated habitat of marbled salamanders. The atlas is available from the Division and from local conservation commissions. When a proposed project will occur within an Estimated Habitat, a copy of the project proponent's Notice of Intent to the local conservation

commission must be forwarded to the Division. Within 30 days of receipt of the Notice of Intent, Division staff determine: 1) whether the proposed project would occur within actual habitat of a rare species; and, if so, 2) whether the proposed project will have any "short or long term adverse effects" on that wetland habitat. The Division submits their opinion to the applicant, the local conservation commission, and the Department of Environmental Protection. The Division's opinion is presumed correct, although it may be rebutted by clear evidence to the contrary.

The important wildlife habitat functions protected under the WPA are: feeding, breeding, migrating, overwintering, and finding shelter. Therefore, adverse impacts to habitats supporting these activities are not permitted. Replicating habitat for wetlands wildlife and moving animals to new habitat are not permitted because impacts to existing habitat still occur. According to the Department of Environmental Protection's rare species policy, "habitat replication, relocation of individual animals, or other proposed measures purported to offset adverse effects shall not be permitted because these activities cannot meet the performance standard of no adverse short or long term effect on the habitat of the local population" (DEP Rare Species Policy 90-2).

Table 3. Resource Areas (pursuant to Massachusetts Wetlands Protection Act) and associated habitat functions provided for marbled salamanders.

	Life stage(s) associated with habitat functions potentially provided					
Resource Area[1]	**feeding**	**breeding**	**migrating**	**overwint-ering**	**shelter**	**Comments**
Land Under Water Body	adults juveniles larvae	adults eggs	adults juveniles	larvae	adults juveniles larvae	A fish-less pond and its buffer zone can provide breeding and upland habitats.
Isolated Land Subject to Flooding (ILSF)	adults juveniles larvae	adults eggs	adults juveniles	larvae	adults juveniles larvae	ILSF can provide habitat if it contains or is near breeding habitat.
Bordering Land Subject to Flooding (BLSF)	adults juveniles larvae	adults eggs	adults juveniles	adults juveniles larvae	adults juveniles larvae	BLSF can provide habitat if it contains or is near breeding habitat.
Bordering Vegetated Wetlands (BVW)	adults juveniles larvae	adults eggs	adults juveniles	adults juveniles larvae	adults juveniles larvae	BVW can provide habitat if it contains or is near breeding habitat.
Riverfront Area	adults juveniles larvae	adults eggs	adults juveniles	adults juveniles larvae	adults juveniles larvae	A Riverfront Area can provide habitat if it contains or is near breeding habitat.

1 Resource Areas (except Isolated and Bordering Lands Subject to Flooding) include a 100-foot upland buffer zone in which activities can be regulated if predicted to adversely affect the Resource Area (the wetland) itself. Riverfront Areas consist of adjacent uplands up to 200 feet from the mean high water line of a river or perennial stream. The uplands within the Riverfront Area are considered part of the Resource Area.

Assessing Impacts Under the WPA – To expedite regulatory reviews of large projects, projects with direct wetland alterations, and projects with significant buffer zone loss, applicants should follow the guidelines below.

- Applicants are strongly encouraged to conduct rare wildlife habitat evaluations prior to filing a Notice of Intent. Such evaluations are more likely to expedite the review process if conducted by a wildlife biologist with proven experience and expertise conducting surveys for the target species, in this case, the marbled salamander. The applicant should use the information provided in the evaluation to determine whether his or her project would adversely affect rare species habitat.

- Submit the full Notice of Intent to the Division, including plans, stormwater management forms and supporting data, wetland delineation forms, any wetland assessments, and any wildlife habitat evaluations. Classifying wetland types according to Cowardin et al. (1979) will help facilitate the Division's review. Alternative analysis reports, as required under the Rivers Protection Act, must be provided.

- Clearly delineate boundaries of proposed work on a U.S.G.S. topographic map. Avoid drawing broad circles or using arrows to indicate the project locus.

- Provide plans that show the entire proposed project on one page, including streets and other landmarks. Plans drawn at a scale of 1:40 are often easiest to interpret. Delineate the limit of clearing on plans and show grading, limit of lawn, and all other project components.

- Delineate wetland Resource Areas, including Riverfront Areas, on plans. Make sure Bordering Vegetated Wetland flag numbers are clearly visible on plans. Delineate wet depressions that may be state or federal wetlands on plans.

- Provide ground-level photographs that characterize wetland types within and near the impact area(s). Label photographs and cross-reference them on 1:40 scale plans. Providing a 1:12,000 scale, color-infrared, aerial photograph (taken when leaves are off trees) with the subject property clearly marked is recommended.

- Provide land-use information for the site and neighboring lands. Include residential and commercial development, roads, agricultural land, and active or abandoned gravel pits. Demarcate these areas on the plans, if possible.

- Include detailed erosion and sedimentation control plans, particularly for sites with steep topography and for projects that will disturb large amounts of upland adjacent to wetlands.

Submit to the Division any new or revised information presented to the Conservation Commission during the hearing process.

Massachusetts Endangered Species Act – The Massachusetts Endangered Species Act (MESA) (MGL c. 131A) prohibits the "taking" of any species of animal or plant listed as Endangered, Threatened, or Species of Special Concern. For animals, "taking" is defined as: "to harass, harm, pursue, hunt, shoot, hound, kill, trap, capture, collect, process, disrupt the nesting, breeding, feeding, or migratory activity or attempt to engage in any such conduct, or to assist in any such conduct" (321 CMR 10.02). This broad definition of "take" allows regulatory protection to be provided to individual marbled salamanders as well as to their wetland and upland habitats.

Under certain circumstances, the Division of Fisheries and Wildlife may grant a permit allowing the "take" of state-listed species. Such "Conservation Permits" are granted only under the following circumstances (321 CMR 10.04(3)): 1) when there are no reasonable alternatives to the proposed project; 2) when the project has been modified to minimize impacts to rare species and their habitats; and 3) when the project has been designed in such a way as to provide a "net benefit" to the population(s) of affected species.

Assessing Impacts under MESA – The Division may request additional site-specific information to aid in its regulatory review of proposed projects. This will be especially true for requests for Conservation Permits that allow limited take of marbled salamanders under MESA. Although 1 to 2 years of additional data collection is unlikely to describe all habitats used by a local population of marbled salamanders, it is likely to contribute information useful to the Division's review process.

In reviewing a project, the Division may request additional information on some or all of the following:

- Presence of marbled salamander larvae at breeding sites – Although all potential breeding sites will *not* contain larvae every year, knowing where they are surviving in a given year will help direct subsequent information-gathering efforts (see below). Larvae are easiest to detect in the spring, when they are much larger than other ambystomatid larvae in the pool. They are also detectable in fall and winter, when they are the only ambystomatid larvae in a pool.

- Directionality (if any) of adults moving to and from their breeding sites – This is usually obtained by fencing a breeding site and placing pitfall traps (e.g. number 12 cans) at 10 m intervals along both sides of the fence line. The fence should be continuous around the entire pool, 0.5 m above the pool's high water level, to the extent topography allows. Traps should include mechanisms for:

    1. allowing the escape of small mammals (e.g. sticks that reach to the top of the trap)
    2. keeping trapped amphibians moist (e.g. sponges at the bottoms of traps)
    3. preventing flooding (e.g. drainage holes punched at the bottoms)

Traps should be checked every morning from August 5 to November 20 to ensure that most immigrants and emigrants are captured.

- Directionality (if any) of juveniles emerging from their pools of origin – This information is collected using the same trapping techniques as for adults, from May 15 to July 15. (Note: Between July 15 and August 5, and between November 21 and May 14, either drift fences and traps should be removed, or trap-checking should continue daily.)

- Mapping habitat types – All known or suspected marbled salamander habitats should be mapped from on-the-ground surveys and aerial photos (1:12,000 minimum scale, color-infrared, leaves-off photos, to increase the likelihood of detecting all vernal pools). Habitat types should be divided into the following general categories: seasonal pools, forested swamps (coniferous dominant, deciduous dominant, and mixed), other wetlands (forested swamps, shrub swamps, marshes, bogs, wet meadows, open water), and forested uplands (coniferous dominant, deciduous dominant, and mixed). Maps should also include roads, high and low density development, and agricultural land. The resulting maps will be used by the Division to assess connectivity among breeding populations.

The Division issues permits for handling and capturing state-listed species in the field and therefore must be contacted before such activities are attempted.

GUIDELINES TO AVOID ADVERSE IMPACTS

Activities that may have adverse effects on marbled salamander habitat and/or may kill or injure adults, juveniles, larvae, or eggs include but are not limited to the following.

- Destroying breeding pools or any portion of them by filling or draining.

- Degrading breeding pools. Examples of degradation include increasing erosion and sedimentation, clearing trees in and around pools, and discharging runoff and contaminants into pools.

- Altering the hydrology of breeding pools (see Skelly et al. 1999). Adding impermeable surfaces nearby, such as pavement and buildings, may increase runoff into the pools while water detention systems can decrease the amount of water that normally reaches a pool. Changing the elevation or grade of land adjacent to pools may also alter the amount of runoff.

- Introducing non-native species to pools. For example, if a pool's hydroperiod increases so that fish can survive in the pool, and fish are introduced, the survival of marbled salamander eggs and larvae may be greatly reduced.

- Destroying or degrading upland habitats. Clear-cutting destroys upland habitat for marbled salamanders (see Deegan and Berkholtz 1989, Raymond and Hardy 1991, deMaynadier and Hunter 1995, deMaynadier and Hunter 1999) as does the removal of

substrates for both salamanders and their prey, such as logs, rocks, and leaf litter. Clear-cutting and substrate removal alter the microclimate on the forest floor. Because Ambystomatid salamanders may depend on small mammals for their burrows (Williams 1973, Semlitsch 1981, Madison 1997), destruction and degradation of small mammal habitat may adversely impact marbled salamanders.

- Adding sources of direct mortality in upland or breeding habitats. Examples include the removal or disturbance of burrowing substrates, the addition or increase of vehicular traffic, and the introduction or increase of environmental contaminants, such as pesticides, fertilizers, contaminants from malfunctioning septic systems, and runoff from roadways (see Lefcort et al. 1997, Diana and Beasley 1998).

- Impeding connectivity between upland, breeding, or dispersal habitats (see Reh and Seitz 1990, Gulve 1994, Dodd and Cade 1998, Gibbs 1998, deMaynadier and Hunter 1999). Roads, walls, curbs, clear-cuts, catch basins, and waterways are examples of impediments to salamander movement.

Because marbled salamanders travel between habitat features that are hundreds of meters apart (Table 2), the activities listed above have the potential to adversely affect habitat or cause "take" of marbled salamanders if they occur up to 1 km from documented salamander sightings. However, not all development activities within the range of maximum movement are likely to adversely affect actual habitat areas or to cause a taking. Each proposed project will be reviewed separately by the Division, and consideration will be given to site-specific conditions, the nature and extent of the proposed activity, the extent and quality of local salamander habitat, and knowledge of both the general ecology and local status of marbled salamanders.

LITERATURE CITED

Anderson, J.D. 1967. *Ambystoma opacum*. Catalog of American Amphibians and Reptiles. American Society of Ichthyologists and Herpetologists.

Bishop, S.C. 1941. The salamanders of New York. New York State Museum Bulletin 324:134-154.

Bishop, S.C. 1943. *Handbook of Salamanders*. Cornell University Press, Ithaca and London.

Cowardin, L. V. Carter, F. Golet, and E. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service. FWS/OBS-79/31. 103 pp.

Deegan, B. and J. Berkholtz. 1989. Eight new breeding sites of the salamander *Ambystoma opacum* in Bristol County, Massachusetts. Unpublished report to Massachusetts Natural Heritage and Endangered Species Program, Division of Fisheries and Wildlife. Report 89-2.

deMaynadier, P.G. and M.L. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews 3:230-261.

deMaynadier, P.G. and M.L. Hunter. 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. Journal of Wildlife Management 63(2):441-450.

Diana, S.G. and V.R. Beasley. 1998. Amphibian Toxicology. Pp. 266-277 in M.J. Lannoo (ed.), *Status and Conservation of Midwestern Amphibians*. University of Iowa Press.

Dodd, C.K. and B.S. Cade. 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. Conservation Biology 12(2):331-339.

Douglas, M.E. and B.L. Monroe. 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). Copeia 1981(2): 460-463.

Gibbs, J.P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. Journal of Wildlife Management 62:584-589.

Gulve, P.S. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. Ecology 75(5):1357-1367.

King, W. 1935. Ecological observations on *Ambystoma opacum*. Ohio Journal of Science 35(1):4-15.

Krenz, J.D. and D.E. Scott. 1994. Terrestrial courtship affects mating locations in *Ambystoma opacum.* Herpetologica 50(1):46-50.

Laan, R. and B. Verboom. 1990. Effects of pool size and isolation on amphibian communities. Biological Conservation 54:251-262.

Lefcort, H., Hancock, K.A., Maur, K.M. and D.C. Rostal. 1997. The effects of used motor oil, silt, and the water mold *Saprolegnia parasitica* on the growth and survival of mole salamanders (Genus Ambystoma). Archives of Environmental Contaminant Toxicology 32(4):383-388.

Madison, D.M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. Journal of Herpetology 31:542-551.

Morris, M.A. 1991. Breeding biology and larval life history of four species of *Ambystoma* (Amphibia: Caudata) in east-central Illinois. Illinois Natural History Survey Bulletin 34:402.

Oliver, J.A. 1955. The Natural History of North American Amphibians and Reptiles. D. Van Nostrand Co., Princeton, New Jersey.

Petranka, J.W., J.J. Just, and E. C. Crawford. 1982. Hatching of amphibian embryos: the physiological trigger. Science 217:257-259.

Petranka, J.W. 1990. Observations on nest site selection, nest desertion, and embryonic survival in marbled salamanders. Journal of Herpetology 24(3):229-234.

Raymond, L.R. and L.M. Hardy. 1991. Effects of a clearcut on a population of the mole salamander, *Ambystoma talpoideum*, in an adjacent unaltered forest. Journal of Herpetology 25:509-512.

Reh, W. and A. Seitz. 1990. The influence of land use on the genetic structure of populations of the common frog (*Rana temporaria*). Biological Conservation 54: 239-249.

Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392:491-494.

Semlitsch, R.D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Canadian Journal of Zoology 59:315-322.

Semlitsch, R.D., D.E. Scott, J.H.K. Pechmann, and J.W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. Pp. 217-248 in *Long-Term Studies of Vertebrate Communities*. Academic Press, Inc.

Semlitsch, R.D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology 12(5):1113-1119.

Semlitsch, R.D. and J.R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12(5):1129-1133.

Scott, D.E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. Ecology 71(1):296-306.

Scott, D.E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology 75(5):1383-1396.

Scott, D.E. and M.R. Fore. 1995. The effect of food limitation on lipid levels, growth, and reproduction in the marbled salamander, *Ambystoma opacum*. Herpetologica 51(4):462-471.

Shoop, C.R. and T.L. Doty. 1972. Migratory orientation by marbled salamanders *(Ambystoma opacum*) near a breeding area. Behavioral Biology 7:131-136.

Skelly, D.K., E.E. Werner, and S.A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80(7):2326-2337.

Stenhouse, S.L. 1985. Migratory orientation and homing in *Ambystoma maculatum* and *Ambystoma opacum*. Copeia 1985(3):631-637.

Stenhouse, S.L. 1987. Embryo mortality and recruitment of juveniles of *Ambystoma maculatum* and *Ambystoma opacum* in North Carolina. Herpetologica 43(4):496-501.

Taylor, B.E. and D.E. Scott. 1997. Effects of larval density dependence on population dynamics of *Ambystoma opacum*. Herpetologica 53(1):132-145.

Williams, P.K. 1973. Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma*. Unpublished PhD. dissertation, Indiana University.